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LIFE CYCLES AND DIAPAUSE

Insect Development: Photoperiod and Temperature Control.—Victor A. Zaslavski. 1988. Springer-Verlag, Berlin, xi + 187 pp. Hardbound $99.95.

The topic of this book is much narrower than the general title of "Insect Development: Photoperiodic and Temperature Control" might indicate. Make no mistake about it, this is a book on diapause. The broader issue of the role that temperature and photoperiod play in other developmental processes is dismissed, on page 11, by the statement, "Mathematical expression of these dependencies can be found in ecological manuals." Although this is a book about diapause, don't expect deep physiological insights into the processes involved. The approach taken is what has been described in the physical sciences as *phenomenological.* Within these limits, however, I believe this is an important contribution to the literature on diapause, following the honorable tradition of contributions that phenomenological models have made in areas such as physics.

Zaslavski has organized his book into three chapters. The first is primarily introductory in nature. The second begins to develop the underlying theme of the phenomenological model, and the third states the form of the model and applies it to examples introduced in the first chapter. My review will be structured according to his organization.

The objective of the first chapter is to lay the empirical groundwork for the subsequent model by defining terms, providing a basic classification scheme for photoperiodic reactions, and to illustrate the diversity and complexity of the photoperiodic response by describing numerous experimental results. The abundance of examples is valuable if for no other reason than providing an introduction to the rich literature on diapause, and in particular, the Russian literature that might not be familiar to Western readers. There is, however, a major problem with the first chapter. It is difficult going, almost to the point of brutality. I suspect that many readers, even those with serious interests in diapause, will become frustrated and

give up. This problem arises from several sources. Diapause, and its control by the interaction of photoperiod and temperature, is an inherently complex subject. Confounding this complexity is Zaslavski's (or translator Vasilyev's) choice of words used for his definitions. The relationship between the common use of a word and the phenomenon described is occasionally obscure and sometimes misleading. A glossary of terms would have been extremely useful, and I advise readers to make one as they progress through this chapter. Some of the problems with definitions undoubtedly resulted in the process of translation from the Russian. Vasilyev's translation sometimes leads to archaic and/or arcane usage.

Throughout the book, but particularly in the first chapter, Zaslavski's figures are often confusing, although I must admit that with persistence they invariably led to a more complete understanding of his narrative. Additionally, figures often augment text discussion that may be several pages removed from placement of the figure, and I caution the reader to avoid the temptation of trying to understand a figure before it is discussed in the text. Most figure captions are not self-contained. Finally, the sheer weight of examples in the first chapter is formidable. Through use of a wide diversity of empirical examples, Zaslavski intends to make a point, but it may be overkill.

The dominating theme of the first chapter is the complexity of insect diapause and seasonality. By the time the reader has finished the first chapter, it is patently obvious that a conceptual model of diapause is an absolute necessity to avoid the morass of a seemingly infinite variation on the theme of seasonality. This is, of course, the reaction that Zaslavski anticipated. He has, in a sense, set the reader up for what follows in the remaining two chapters.

In the first 3 pages of Chapter 2, Zaslavski makes an eloquent argument for a unified physiological basis for diapause control in the insects. He goes on to present many experimental examples. However, as opposed to the examples in Chapter 1, the underlying theme of Chapter 2 is one of unification. Zaslavski bases his unification on a two phase process (a "dual control mechanism"). His historical review of the development of a duality concept of diapause is quite good (pp. 114–117) and logically results from the preceding empirical data. Duality, leading to a "profound relationship between inductive and spontaneous processes in seasonal development of insects," is reinforced by discussion in the remainder of this chapter.

Actual formulation of Zaslavski's two phase model is the subject of Chapter 3. This formulation is composed of two parts. The first, on pages 129–131, sets out the quantitative basis for the expression of photoperiod. The second, on pages 133–136, defines the components of the model and describes their properties and interconnections. A physiological basis underlies both discussions. As previously noted, Zaslavski's approach is descriptive rather than mechanistic. For example, the basic shape of the photoperiodic threshold curve (a 2 hump curve, or perhaps more descriptively, a valley and a hill) as presented on page 137 is absolutely necessary for proper functioning of the model (e.g., Figs. 84, 86, 87, 88, and 89). This specific shape results from integrating the area under two simple curves describing the photoperiod effect on enzyme synthesis. The temporal relationship between these two curves in turn results in the appropriate shape for the photoperiodic response. The result of all this is a simple model that integrates the effects of photoperiod and temperature and also provides a unified description for a complex array of observed photoperiodic

responses. These results are important enough that I, for one, plan to discuss the physiological basis of the model in more detail with a qualified specialist.

Although Zaslavski does indeed provide a synthetic model for diapause, I was personally disappointed that he does not provide a formal mathematical statement of that model. A mathematical statement of the model would have made it easier for me to understand the arguments that Zaslavski uses to develop his model and to convince myself that his consequences logically followed from his assumptions. More importantly, mathematics provides a formal mechanism to test (validate) a model. Zaslavski makes an attempt at validation through a process he terms "prediction." I disagree with his use of the term. Zaslavski has used his model to describe various patterns of observed photoperiodic response and seasonality (see pages 137–158). Clearly, his model is flexible and can describe a wide array of empirical diapause patterns. However, just as clearly, this is not prediction in the prospective sense of the word. I have a hunch that Zaslavski's model as stated is overparameterized, in other words, a model that is flexible in descriptive capabilities but lacks predictive power. Use of his model for prediction will require constraints that may be implicitly included in his discussion but that were not explicitly stated.

The topic of Zaslavski's book is an important one. Appropriate timing of life history events is arguably the single most important adaptation of insects living in seasonal environments. Additionally, the appropriate modeling of diapause assumes economic importance because its termination initiates subsequent phenology. Accurate prediction of insect phenology is often critical to effective control. Given this importance, Zaslavski makes a significant contribution to the literature on insect ecology. Almost 30% of the 442 articles cited are in Russian. A significant proportion of the remaining articles are in non-English language journals. By using this literature to build the empirical basis for his model, Zaslavski provides insights into current trends in diapause research in the USSR. Considering that both the US and the USSR are notoriously xenophobic in their scientific outlook (e.g., Garfield, 1988), books such as Zaslavski's can do much to promote a scientific *glasnost*.

The second significant contribution is the major reason Zaslavski undertook this project, and that is to present a dual phase model that unifies photoperiodic and temperature control of diapause. Zaslavski is largely successful in this presentation. As previously stated, I am personally disappointed in the lack of mathematical rigor in his formulation of the model. In my opinion, the rigorous, unambiguous mathematical statement of his model would make an excellent Chapter 4, and the application of the model for parameter estimation would make an excellent Chapter 5. Perhaps all this is just to say that Zaslavski's is not the last word on the subject, and there is work yet to be done for the rest of us.

Zaslavski's work is particularly useful for establishing priorities in diapause research, and he does so on many occasions. For example, on page 139 regarding the interrelationship between temperature and photoperiod, he states, "Temperature affects the commanding centers of poikilotherm organisms directly and thus inevitably. In contrast, to perceive the daylength a mechanism of photoperiodic clock is necessary, the presence or functional activity of which seems to be nonobligatory, since photoperiodically neutral species exist. Therefore, the temperature reaction should be considered both separately and in combination with the photoperiodic one." Zaslavski also makes a serious attempt to place diapause within the total eco-

logical matrix of factors impinging on the success of a species. By doing this, his book is motivation for collaboration between insect physiologists, insect ecologists, and mathematical modelers. It is only through such collaboration that we can expect to make progress toward a more complete understanding of diapause.

A final note on the cost of this book is probably in order. Translations of technical books with limited distribution are notoriously expensive. At a price of $100 for a book of 187 pages (including References and Index) "Insect Development" is no exception to this rule. I for one, however, am glad that Springer-Verlag is willing to undertake such ventures, and if such prices are necessary, then so be it. I anticipate that I will refer often to this book in my work involving diapause and insect seasonality. I also anticipate significant insights will be gained into procedural methods for modeling such processes. My advice to serious researchers in the area of diapause and insect ecology is to buy the book and then make it widely available to students and others who might find it prohibitively expensive.—*Jesse A. Logan, Department of Entomology and Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.*

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The Evolution of Insect Life Cycles.—F. Taylor and R. Karban (eds.). 1986. Springer-Verlag, New York, 287 pp. $64.00.

This book is a collection of sixteen papers on the evolution of life cycles in insects. The papers are modified from a symposium at the XVII International Congress of Entomology in 1984. The stated goal of the volume is ". . . to provide a comprehensive view of current research on insect life cycles . . . ." The book is organized into four sections: Geographical Patterns in Insect Life Cycles (5 papers), Diversity of Life Cycle Patterns (6 papers), Mechanisms of Insect Life Cycle Evolution (4 papers) and Concluding Remarks (1 paper); however, many of the papers are appropriate for more than one section.

The book addresses several important issues in the study of insect life histories, among them the reality of environmental uncertainties which can produce considerable year to year variation in selection pressures. Several chapters discuss this point in both theoretical and empirical terms, as well as the consequences for genetic variability of life history traits. Several other papers consider exceptions to generalizations about life histories. For example, A. Shapiro reports that r- and K-type traits do not consistently occur at a taxonomic level; however, they do correspond to what is known of the ecology of the organisms and the presumed selection pressures.

Several of the chapters discuss genetic aspects of life histories. This is a crucial issue in the study of the evolution of life histories and I felt a general weakness of some of the papers was implicit assumptions about genetic systems. There seems to be a tendency for authors to infer past selection from present patterns. For example,